FACTORS INFLUENCING POSTFIRE SPROUTING VIGOR IN THE CHAPARRAL SHRUB *ADENOSTOMA FASCICULATUM*

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Abstract

Several indices characterizing prefire size and structure of *Adenostoma fasciculatum* shrubs were measured in a chaparral stand slated for an experimental burn. Burl concentrations of total nonstructural carbohydrates (TNC) were also assessed. Following the fire, aboveground biomass production during the first postfire year was determined. In addition, a shading experiment was implemented after the fire to assess the contribution of current photosynthesis of sprouts to postfire sprouting vigor.

Postfire biomass production was positively correlated with prefire shrub size, but negatively correlated with prefire dead stem area and percent dead stem area. Burl TNC concentrations showed no patterns with respect to prefire shrub size, the percent dead stem area, or postfire sprouting vigor. Reducing incident sunlight with shadecloth resulted in significant reductions in postfire biomass production. Our results suggest that stands of *A. fasciculatum* having high components of standing dead biomass sprout less vigorously after fire.

Substantial biomass levels and prolonged seasonal drought combine to ensure that fire plays an important role in the shrub-dominated chaparral of California. Although the "natural," pre-European fire frequency in this vegetation is the subject of much debate, it is often said that stands of chaparral burned on the average of every 20–40 years prior to modern fire suppression practices (e.g., Philpot 1977; Minnich and Howard 1984). Some evidence indicates that fire suppression practices may have resulted in fewer, but larger and more destructive fires in recent decades (Minnich 1983), because fire suppression may have led to a preponderance of old stands of chaparral with higher proportions of dead fuels. Such old stands might be expected to burn more destructively in a wildfire than younger stands with less dead fuel accumulation. In any case, the current juxtaposition of chaparral with the ever-encroaching urban areas of southern California has necessitated the adoption of prescribed burning by land management agencies to reduce fuel loads and fire hazard. Certainly the need has never been greater for basic information on how chaparral species respond to fire.

Many chaparral shrub species sprout vigorously after fire, a characteristic that likely confers an enormous advantage to sprouting

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species compared to nonsprouting, obligate seeding species. Sprouting shrubs have mature root systems, with their carbohydrate and nutrient reserves, as well as greater access to soil water and nutrients compared to seedlings. Sprouting shrubs suffer little of the drought-induced mortality that is common among postfire seedlings (Kummerow et al. 1985).

Despite the importance of postfire sprouting in the California chaparral, little is known about the controls of sprouting success and vigor. In a study of *Adenostoma fasciculatum* H. & A. (Rosaceae) (chamise) (nomenclature follows Munz 1974), a widespread sprouting shrub species in the California chaparral, Jones and Laude (1960) concluded that root, shoot, and root crown (burl) total nonstructural carbohydrate (TNC) levels were influential in chamise growth rates after mechanical cutting, since little fall and winter growth (when TNC levels were low) was observed even when temperature and moisture conditions were favorable. However, Radosevich and Conard (1980) have shown that the lower initial growth rates of chamise shrubs burned when TNC levels were low did not result in shorter shrubs after two seasons of growth; hence, current photosynthesis of sprouting shoots, and not belowground TNC levels only, may also influence postfire sprouting vigor.

A major remaining deficit of information regarding sprouting is whether prefire shrub condition, as expressed by shrub size and the amount of standing dead biomass, influences postfire sprouting vigor. If land managers using prescribed burning are to contend with an increasing proportion of older stands of chaparral with higher levels of standing dead biomass, then it will become increasingly important to understand whether shrubs in different prefire condition respond to fire differently.

We investigated three aspects of the response of sprouting *Adenostoma fasciculatum* to fire. First, we were interested in determining whether prefire shrub condition, as assessed by shrub size and the amount of standing dead fuels in the shrub, influenced postfire ⌐prouting vigor. We therefore examined the relationships between several indices of prefire shrub size and structure, and postfire sprouting vigor. Second, we were interested in exploring further the influence of prefire shrub storage carbohydrate (TNC) levels on postfire sprouting vigor, and how such TNC levels might differ in shrubs of different prefire condition. Third, we evaluated the contribution of current photosynthesis of sprouting shoots to postfire sprouting vigor in a shading experiment.

Materials and Methods

Structural characteristics were recorded for 73 *Adenostoma fasciculatum* (chamise) shrubs growing in a 54-year old (i.e., 54 years

since the previous fire) mixed chaparral community scheduled for an experimental burn in the autumn of 1982. The stand was located on a north-facing slope (1400 m elevation) at the Sky Oaks Biological Field Station in northeastern San Diego County, California. The total size of the study area was about 0.25 ha (50 × 50 m). Chamise shrubs in this stand could be found in a variety of sizes and with a variety of levels of standing dead biomass. Co-occurring shrub species included *Ceanothus greggii, Quercus dumosa,* and *Adenostoma sparsifolium.*

Chamise shrubs were selected by establishing transects on the study slope at 10 m intervals, and points along the transect were chosen at random. Data were collected from the chamise shrub nearest to the random point. For all 73 chamise shrubs the following data were taken: (1) length and width measurements of each burl (enough soil was removed from around the burl so that the true shape could be ascertained, since burls were often irregular in shape; the longest axis was chosen as the length, and the axis perpendicular to the length was chosen as the width); (2) number and diameter of all live and dead stems at 10 cm height above the burl; and (3) canopy length and width measurements, using the same method described above for measuring burl dimensions.

Burl length and width measurements were used to calculate burl area, an index of burl size. Burl volume was not measured since its determination would require destructive sampling. Similarly, canopy length and width measurements were used to calculate a rough estimate of canopy area, an index of shrub size. Stem diameters were used to calculate stem areas, which were then summed across all stems to obtain total live and dead stem areas for each shrub.

After collection of shrub structural data, a small sample of woody tissue was removed from each burl for total nonstructural carbohydrate (TNC) analysis. Samples (1–2 g dry weight) were removed by drilling into the burl approximately 1 cm deep and collecting the drill shavings. Since burls were composed of both functional and nonfunctional material, burl samples were consistently taken near the base of live stems to obtain samples from functional (i.e., nondecaying) woody tissue. More thorough characterization of burl TNC status would have entailed greater potential perturbation to the shrubs' postfire sprouting. Sampling was completed during a six week period (early October to mid November), and tissue was collected at whatever time of day a particular shrub was visited. Samples were dried in a forced draft oven (57°C) for 48 hr, placed in a sealed vial, and stored until analyzed. Total nonstructural carbohydrates were quantified using a Technicon autoanalyzer following the procedure of Smith (1969).

Because of various weather factors, the scheduled experimental burn was postponed until January 1984, approximately one year

after the data above were collected. Although changes in burl TNC concentrations probably occurred during this interval, it is likely that TNC relationships among the shrubs of various sizes and conditions remained unchanged. Certainly shrub structural characteristics did not change ostensibly during this time interval, and any trends in relative shrub condition would likely occur at a time scale longer than one year in this 54-year-old stand. We cannot, however, determine whether or not significant changes in relative shrub condition occurred during the delay.

An off-season burn was deemed necessary to reduce fire hazards, and the burn was carried out under cool (10–20°C) and cloudy conditions. The burn was, however, complete over the 0.25 ha study area. Shrub growth is negligible at this elevation in the winter, so shrubs had not yet invested in any new growth.

All shrubs were numbered and tagged with stainless steel tape before the fire. In October 1984, after one postfire growing season, total aboveground sprout biomass (excluding the charred remains of branches) of each shrub was harvested, dried (40–50°C for 5–7 days), and weighed.

In May 1984, prior to any postfire sprouting, each of 17 shrubs (randomly chosen from among the original sample of 73 shrubs) was enclosed within an approximately 50 × 50 cm frame (exact shape depended on burl dimensions) onto which shadecloth was fastened to form a canopy over each burl, and which enclosed the burl on three sides. Shadecloth was of a standard nursery variety affording approximately 84% shade (16% transmittance). The east side of these shadecloth "tents" was left open so all burls would receive full sunlight for a part of the morning. In this way, peak irradiance was not inhibited to an extent that would cause the shoots to etiolate. Total postfire aboveground sprout biomass of the shaded individuals was also determined in October 1984.

Of the 73 shrubs described before the experimental burn, 15 were cut by fire crews a few days before the fire, and two shrubs did not survive the fire. The final sample consisted of 56 shrubs, 17 of which were enclosed in shadecloth tents (hereafter referred to as the "shaded shrubs"), while 39 were assigned to be the reference plants (hereafter referred to as the "unshaded shrubs").

Prior to calculating correlation coefficients, dependent variables (production and production per unit shrub size) were plotted against each measure of shrub structure to determine whether relationships were linear or non-linear and to evaluate subjectively the strength of the relationship. If statistically significant correlation coefficients were based on a few outliers, the "significance" of the relationship was not accepted. All relationships that were determined to be significant appeared to be linear.

One measure of shrub structure, percent live stem area, was arc-

Table 1. Means and Ranges of Several Variables Measured for Unshaded and Shaded *Adenostoma fasciculatum* Shrubs before a Controlled Burn, Plus the Mean and Range for Aboveground Net Postfire Biomass Production of These Shrubs during the First Postfire Growing Season (May to October). No significant differences were found between unshaded and shaded shrubs for any of the variables except postfire biomass production (t-test, $\alpha = 0.05$).

		Unshaded shrubs (n = 39)	Shaded shrubs (n = 17)
Burl area (cm²)	Mean	833.6	609.2
	Range	(143–2805)	(150–1748)
Canopy area (cm²)	Mean	18,289	17,729
	Range	(3200–51,750)	(440–47,385)
Live stem area (cm²)	Mean	38.8	40.8
	Range	(5–109)	(7–130)
Dead stem area (cm²)	Mean	14.3	12.5
	Range	(0–41)	(0–73)
Total stem area (cm²)	Mean	53.1	53.3
	Range	(12–129)	(7–203)
Live stem area (%)	Mean	70.5	80.2
	Range	(30–100)	(49–100)
Live stems (#)	Mean	9.2	10.7
	Range	(1–22)	(2–24)
Burl TNC conc.	Mean	76.1	77.6
(mg TNC/g dry wt.)	Range	(49–107)	(57–105)
Production	Mean	362.0	161.1
(g dry wt.)	Range	(0–873)	(7–423)

sine-square root transformed (Neter et al. 1985), which, based upon inspection of residual plots, appeared to stabilize the variance. Homogeneity of variance was assessed for all other variables, based upon inspection of residual plots.

Stepwise multiple regression was used as a tool to ascertain the most influential variables in an effort to construct models predicting shrub biomass production and relative biomass production as a function of prefire shrub structure. In all cases, adding more independent variables to the model did not result in adequate improvements over the single variable models. Since coefficients of determination were never high enough to yield a solidly predictive relationship, the effort to construct "best fit" models was abandoned.

Results

Means and ranges of all prefire indices are shown in Table 1 for both shaded and unshaded shrubs. No significant differences were found between shaded and unshaded shrubs for any prefire (and pretreatment) index (t-test, $\alpha = 0.05$).

Unshaded shrubs. Postfire aboveground sprout biomass production in unshaded chamise shrubs was significantly associated with several indices of prefire shrub size, specifically the number of live stems, burl area, canopy area, live stem area, total stem area, and the (arcsine-square root transformed) percent live stem area (Table 2). Live stem area produced the highest correlation coefficient with postfire biomass production ($r = 0.77$, $P < 0.001$; Table 2). Postfire biomass production was not associated with prefire dead stem area nor with prefire burl TNC concentration.

Although biomass production was significantly correlated with burl area and canopy area, these two measures of prefire shrub size were not significantly correlated with one another. Burl area was positively correlated with live ($r = 0.55$, $P < 0.0003$) and total stem area ($r = 0.67$, $P < 0.0001$). Canopy area was significantly associated with live ($r = 0.54$, $P < 0.0007$) and total stem area ($r = 0.48$, $P < 0.003$), and with the number of live stems ($r = 0.38$, $P < 0.023$). Neither burl area nor canopy area was significantly associated with the proportion of live stem area, indicating that shrub size was not related to the proportion of live (or dead) stem area.

Prefire burl TNC concentrations showed no significant correlations with any indices of prefire shrub size or structure, nor with postfire biomass production.

In order to control for shrub size in considerations of postfire sprouting vigor, we derived two measures of postfire unit production by dividing biomass production by prefire burl area and prefire canopy area (Table 2). Unlike simple production, biomass production/burl unit area was significantly associated with only two measures of prefire shrub structure—negatively correlated with dead stem area and positively correlated with (arcsine-square root transformed) percentage live stem area (Table 2). Interestingly, biomass production/burl unit area was not correlated with live stem area, which had the best association with simple production, whereas simple production was not correlated with dead stem area, which had the best association with biomass production/burl unit area. Biomass production/canopy unit area was positively associated with prefire live stem area, as well as with prefire burl area and the number of live stems.

Shaded shrubs. No significant correlations were found between postfire production and any prefire shrub index for shaded shrubs, perhaps in part because the sample size is smaller ($n = 17$, compared with $n = 39$ for the unshaded shrubs).

Aboveground net biomass production in the season following the experimental burn was significantly greater for the unshaded shrubs compared with the shaded shrubs (t-test, $P < 0.0001$) (Table 1). The unshaded shrub average biomass production was 2.2 times greater

TABLE 2. CORRELATION COEFFICIENTS OBTAINED FROM CORRELATING POSTFIRE ABOVEGROUND BIOMASS PRODUCTION AND PRODUCTION PER UNIT PREFIRE SHRUB SIZE (PRODUCTION PER UNIT BURL AREA AND PRODUCTION PER UNIT CANOPY AREA) WITH SHRUB PARAMETERS MEASURED BEFORE THE FIRE (TOTAL NONSTRUCTURAL CARBOHYDRATE CONCENTRATION, OR TNC, THE NUMBER OF LIVE STEMS, BURL AREA, CANOPY AREA, LIVE STEM AREA, DEAD STEM AREA, TOTAL STEM AREA, AND THE PERCENT LIVE STEM AREA). Percentage live stem area data were transformed (arcsine-square root) before calculating correlation coefficients. "ns" = non-significant; "*" = variables collinear.

	TNC	# live stems	Burl area	Canopy area	Live stem area	Dead stem area	Total stem area	% live stem area
Production	ns	0.69 $P < 0.001$	0.43 $P < 0.006$	0.45 $P < 0.005$	0.77 $P < 0.001$	ns	0.64 $P < 0.001$	0.40 $P < 0.011$
Production/burl area	ns	ns	*	ns	ns	−0.60 $P < 0.001$	ns	0.49 $P < 0.002$
Production/canopy area	ns	0.50 $P < 0.002$	0.41 $P < 0.012$	*	0.36 $P < 0.032$	ns	ns	ns

than the average biomass production of the shaded shrubs for the postfire growing season of May to October 1984. Biomass production/burl area was also significantly greater for the unshaded compared to shaded shrubs (P < 0.014).

DISCUSSION

In this 55-year-old stand (i.e., 55 years since the previous fire), *Quercus dumosa* and *Ceanothus greggii* constituted the majority of the cover and the stand appeared to be vigorous in that most shrubs were tall and leaf area index, although not measured, appeared to be high. Many chamise shrubs had high components of standing dead biomass, however, and over 50% of the total stem area was dead in some individuals. High competition for light on this north-facing slope may have induced much of this stem mortality in the lower, shaded branches. It should be noted, however, that the time elapsed since the last fire approached that sometimes associated with stand senescence in the literature (e.g., Hanes 1971; Rundel and Parsons 1979, 1980).

Chamise shrubs that were large before the experimental fire, as estimated by burl or canopy size, tended to produce more biomass after the fire. Similar results have been observed for chamise growing in the foothills of the Sierra Nevada (Stohlgren et al. 1984). This result may appear somewhat trivial, but nevertheless has important ramifications. A shrub that attains some modicum of canopy dominance before a fire is likely to maintain that dominance after the fire, potentially enabling such individuals to remain large and dominant across multiple fire cycles. However, Keeley (1973) observed that large chamise shrubs sprouted less frequently after wildfires, perhaps due to heart rot (cf. Stohlgren et al. 1984). Whether similar relationships between shrub size and sprouting exist for other species of sprouting shrubs would be interesting to ascertain.

Shrubs having high dead stem area or high proportions of dead stem area (i.e., low percentage live stem area) before the fire tended to produce less sprouting biomass per unit prefire shrub size (as measured by burl area) in the first postfire season. If a high dead biomass component in individual shrubs indicates shrub senescence, as a high standing dead biomass component in stands might indicate stand senescence (e.g., Hanes 1971), then our data show that such "senescing" shrubs tend to recover less vigorously after the fire than shrubs with higher live biomass components. Alternatively, a large dead biomass component in a shrub could simply indicate that it has been weakened by competition. Regardless of the cause, a large prefire dead biomass component indicates a weakened state that is significantly associated with diminished postfire production.

The full range in values of percent live (or dead) stem area was

distributed among shrubs of all sizes, as there was no significant association between proportion of live stem area and burl or canopy area. The observed influence of the proportion of dead stem area on postfire unit production therefore appears to be size independent.

Increased bud mortality during the fire (and the consequent lower postfire sprout production) in shrubs with a high prefire dead biomass component is possible, but seems unlikely given the cool conditions of the fire and the low shrub mortality.

Burl TNC concentrations, which were intended as an index of burl energy reserves, showed no pattern with respect to shrub size, the proportion of dead stem area, or postfire sprouting vigor. Other studies have shown that energy reserves are important in postfire sprouting in chamise (e.g., Jones and Laude 1960; Radosevich and Conard 1980), as well as in *Populus tremuloides* (Shier 1976). We propose four hypotheses for the lack of correlation in our data between postfire sprouting vigor and burl TNC concentrations. First, we had hoped that sampling burl tissue before the fire would provide a tractable index of shrub TNC levels with a minimum of perturbation of the shrubs' postfire sprouting performance. However, the burl may not be an important storage organ. The roots of *Adenostoma fasciculatum* have been shown to contain the greatest concentrations of starch (Jones and Laude 1960). The burl may function largely as a sprouting organ providing protection from the fire for the latent buds (Carrodus and Blake 1970; James 1984; Moreno and Oechel 1991; but compare Mullette and Bamber 1978). Second, shrub TNC levels fluctuate seasonally (Jones and Laude 1960; Shaver 1981). Our burl tissue samples were collected in the autumn when the carbohydrate reserves in chamise may not be replenished from expenditures in spring and summer growth. Perhaps differences in TNC levels among shrubs with differing levels of postfire sprouting are obscured at this time. Third, relationships between burl TNC and shrub structure among the sampled shrubs may have changed during the one year delay between sampling and burning. Fourth, reserve carbohydrates are probably heterogeneously distributed in the burl (James 1984), so single small samples of burl tissue have a low probability of representing the carbohydrate status of the burl. Whatever the reason, the results from our TNC data are inconclusive.

Energy reserves are only one factor which could potentially contribute to postfire sprout production. Results from the shading experiment demonstrate that current photosynthesis of sprouting shoots contributes significantly to postfire aboveground biomass production. While our burl TNC concentration data do not support the notion that reserves are also important in postfire sprouting, other circumstantial evidence suggests that belowground reserves do influence sprouting. First, even with considerable shading, biomass

production was nearly half that of those shrubs in full sunlight. Second, casual observation in July 1985 of a few of those shrubs whose entire aboveground biomass was harvested in October 1984 after one season of postfire growth, revealed that no sprouting had occurred in the second postfire year. Such a total lack of regrowth following both burning and harvesting suggests that either energy reserves or bud primordia can limit postfire sprouting. Repeated herbivory of chamise sprouts has produced similar results (Moreno and Oechel 1991). Perhaps current photosynthesis during the first postfire year accomplishes little toward replenishing those reserves that are utilized in sprouting, but instead simply augments postfire sprout production.

We have shown the potential for prefire shrub size and the proportion of standing dead biomass to influence postfire sprout production in *A. fasciculatum* shrubs. While our data do not demonstrate senescence in chamise shrubs, they provide evidence that stands having many sprouting shrubs with high proportions of standing dead biomass will tend to recover less vigorously after fire, perhaps due to a reduced ability in shrubs in these stands to sequester TNC reserves to support sprouting. Sparks et al. (1993) observed that shrubs in old stands of chaparral sequestered lower proportions of their leaf photosynthate into TNC during the spring, which could affect belowground accumulation of TNC reserves. Such old stands are, of course, likely targets of land managers using prescribed fire to reduce fuel hazards. While the amount of standing dead biomass alone is not a good predictor of chaparral stand age (Paysen and Cohen 1990), the proportion of shrubs having high components of standing dead biomass is nevertheless likely to increase with age for any particular stand; however, the rate at which the increase occurs may vary for different levels of site quality. Hence there may be some incentive to burn chaparral stands before high levels of standing dead biomass are reached, both to reduce fuel hazard and to promote vigorous postfire sprouting. Evidence of reduced sprouting capability in old individuals is also found for some hardwood tree species (Roth and Hepting 1943; Johnson 1977; Kays et al. 1988).

Obviously, other factors are probably also influential in postfire sprouting in the chaparral; our own data for chamise indicate the importance of current photosynthesis of sprouting shoots. Future research should focus on the effects of season and temperature of the prescribed fire. Our experimental burn was carried out under cool and wet conditions (actually a probable scenario for prescribed chaparral burns in general). A summer or fall burn could generate higher temperatures and perhaps increase sprouting shrub mortality to levels observed for chamise elsewhere (Keeley and Zedler 1978; Stohlgren et al. 1984; Moreno and Oechel 1991; only two chamise shrubs were killed in our burn). Finally, the interactions between

postfire sprouting vigor, nutrient availability, and fire temperature (which influences nutrient volatilization; DeBano et al. 1979; Dunn et al. 1979) need to be evaluated to maximize the efficacy of prescribed fire as a management technique in the California chaparral.

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